

CYTOLOGY AND EVOLUTION IN HAMAMELIDACEAE<sup>1</sup>

PETER GOLDBLATT AND PETER K. ENDRESS

IN A RECENT REVIEW of cytology in relation to angiosperm phylogeny, Raven (1976) was able to suggest basic chromosome numbers and to formulate hypotheses on the evolution of many major groups. One of the results of the study was to focus attention on phylogenetically critical genera for which cytological data were unknown. With Raven's encouragement and help, material of several genera critical to the understanding of relationships within the Hamamelidaceae *sensu lato*, and of the Hamamelidales as a whole, were sought for cytological study. These genera included *Disanthus*, *Rhodoleia*, *Exbucklandia*, and *Altingia*. The first three each represent the sole genus in subfamilies of Hamamelidaceae (Disanthoideae, Rhodoleioideae, and Exbucklandioideae, respectively); *Altingia* with *Liquidambar* comprise the Liquidambaroideae. These four subfamilies, together with Hamamelidoideae, comprise the Hamamelidaceae (*sensu* Harms, 1930). Up to the time the study was undertaken,  $x = 12$  had consistently been reported in all seven of the 22 genera of Hamamelidoideae which are known cytologically (TABLE 1), while *Liquidambar* with  $n = 16$  (Santamour, 1972) and *Exbucklandia* with  $n = 32$  (Mehra & Khosla, 1969) stood out in sharp contrast.

## MATERIALS AND METHODS

Diploid counts were made from germinating seedlings of *Rhodoleia teysmannii* and *Altingia excelsa*, material of both having been obtained with the help of Dr. Willem Meijer from Tjibodas Mountain Gardens, Bogor, Indonesia. Root tips for these counts were pretreated in 0.02% aqueous colchicine or 0.003M hydroxy-quinoline for five hours, and were then fixed in 3:1 absolute ethanol: glacial acetic acid. Squashes were made as described by Goldblatt (1976). Counts for *Disanthus cercidifolius* were made from meiotic material, with pollen mother cells being squashed in the usual way and stained in acetocarmine.

## RESULTS

*Disanthus cercidifolius* Maxim.,  $n = 8$ . Material cultivated in Zurich, Switzerland, origin not known, Endress 3528 (z).

*Altingia excelsa* Noronha,  $2n = 32$ . Indonesia, Java, Tjibodas Mountain Gardens, Bogor, Meijer s.n. (no voucher, representative material at BO).

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TABLE 1. Chromosome numbers in Hamamelidaceae.

SPECIES	HAPLOID NUMBER ( <i>n</i> )	REFERENCE
HAMAMELIDOIDEAE		
<i>Corylopsis glabrescens</i> Franch. & Sav.	24	Santamour 1965
<i>C. himalayana</i> Griff.	12	Mehra & Khosla 1969
<i>C. pauciflora</i> Sieb. & Zucc.	12	Anderson & Sax 1935, Santamour 1965
<i>C. platypetala</i> Rehd. & Wils.	12	Santamour 1965
<i>C. sinensis</i> Hemsl.	12	Santamour 1965
<i>C. spicata</i> Sieb. & Zucc.	36	Anderson & Sax 1935, Santamour 1965
<i>C. veitchiana</i> Bean	36	Anderson & Sax 1935, Santamour 1965
<i>C. willmottiae</i> Rehd. & Wils.	24	Santamour 1965
<i>Distylium racemosum</i> Sieb. & Zucc.	12	Sugiura 1936
<i>Fothergilla gardenii</i> Murray	36	Ernst 1963
	24 <sup>2</sup>	Weaver 1969
<i>F. major</i> (Sims) Lodd. (incl. <i>F. monticola</i> )	24 <sup>2</sup> /36	Anderson & Sax 1935
	24 <sup>2</sup> /36	Ernst 1963
	36	Weaver 1969
<i>Hamamelis vernalis</i> Sargent	12	Anderson & Sax 1935
	12	Ernst 1963
<i>H. virginiana</i> L.	12	Ernst 1963
<i>Parrotia persica</i> C. A. Mey.	12	Pizzolongo 1958
<i>Parrotiopsis jacquemontiana</i> Rehd.	12	Anderson & Sax 1935
<i>Sinowilsonia henryi</i> Hemsl.	12	Anderson & Sax 1935
RHODOLEIOIDEAE		
<i>Rhodoleia teysmannii</i> Miq.	12	present work
DISANTHOIDEAE		
<i>Disanthus cercidifolius</i> Maxim.	8	present work
EXBUCKLANDIOIDEAE		
<i>Exbucklandia populnea</i> R. Br. ex Griff.	32	Mehra & Khosla 1969
LIQUIDAMBAROIDEAE		
<i>Liquidambar orientalis</i> Mill.	16	Pizzolongo 1958, Ernst 1963
<i>L. styraciflua</i> L.	15	Anderson & Sax 1935
	16	Pizzolongo 1958
	15, 16	Ernst 1963
<i>L. styraciflua</i> × <i>L. orientalis</i>	16	Santamour 1972
<i>L. styraciflua</i> × <i>L. formosana</i> Hance	16	Santamour 1972
<i>Altingia excelsa</i> Noronha	16	present work

<sup>2</sup> According to Weaver (1969), differing numbers in earlier counts were due to misidentification of the specimen.

*Rhodoleia teysmannii* Miq., 2*n* = 24. Indonesia, Java, Tjibodas Mountain Gardens, Bogor, *Meijer s.n.* (no voucher, representative material at BO).

DISCUSSION

The results of this study stress the fundamental divergence within the Hamamelidaceae, with *n* = 12 basic in Hamamelidoideae and now re-



ported in Rhodoleioideae, and  $n = 8, 16$ , and  $32$  found to be basic not only in Liquidambaroideae and Exbucklandioideae, but now also in Disanthoideae. Similarities in morphology among genera in these two divergent lines are thus likely to be of considerable taxonomic significance. Several characters are typical, although not strictly exclusive, for one group or the other. For example, pinnate leaf venation, stellate hairs, and one (rarely to three) ovules per carpel (except *Rhodoleia*) are found in the  $x = 12$  group, while rather palmate leaf venation, lack of stellate hairs (except *Chunia*), and six or more ovules per carpel occur in the  $x = 8$  group.

A second very striking result was the discovery of  $n = 8$  in *Disanthus*, making this the first diploid in the otherwise polyploid Hamamelidaceae, and in fact the first diploid in Hamamelidales as circumscribed by Cronquist (1968) and Thorne (1974). This strongly supports the ancestral position within Hamamelidaceae usually assigned to Disanthoideae in phylogenetic treatments.

The flower of *Disanthus* shows a unique combination of characters regarded as primitive in the family: bisexuality, pentamery, double perianth, superior ovary, and the presence of several ovules per carpel. On the basis of leaf morphology, Wolfe (1974) comments that of all Hamamelidaceae he examined, *Disanthus* has foliage most similar to other putatively primitive members of its subclass. Furthermore, it forms a link with the  $x = 12$  group, especially with *Hamamelis* and its allies, in inflorescence and flower structure.

The occurrence of a primitive, ancestrally diploid member of Hamamelidaceae makes it probable that the family is not, as previously believed, of polyploid origin. Whether the Hamamelidaceae are regarded in the broad sense, including the Liquidambaroid-Exbucklandioid-Disanthoid line with  $x = 8$ , or in a more restricted sense, including only the  $x = 12$  line, it is clear that the two groups are fundamentally allied, and are derived from a common ancestral stock. Most likely,  $x = 7$  is basic in the family, with early aneuploid decrease to  $x = 6$  and subsequent polyploidy to give rise to the Hamamelidoid-Rhodoleioid alliance, and aneuploid increase to  $x = 8$ , still found in Disanthoideae, with subsequent later polyploidy leading to the Exbucklandioid-Liquidambaroid alliance. It is also possible that either  $x = 8$  or  $x = 6$  is basic, with an aneuploid decrease or increase, respectively.

Significantly, the only other diploids in the Hamamelidiflorae (*sensu* Thorne, 1974), i.e., Casuarinaceae (Casuarinales), Fagaceae, and Betulaceae (Fagales), are *Casuarina* ( $x = 8, 9$  with  $8$  in the more primitive members of the genus) and *Carpinus*, *Ostrya*, and *Ostryopsis* (all  $x = 8$ ) of the Betulaceae-Coryloideae. The occurrence of similar base numbers in Hamamelidaceae and Casuarinaceae is of particular importance since it now makes a relationship between these two plausible on cytological grounds, where previously the low base number in the very specialized Casuarinaceae seemed inconsistent with such a hypothesis.

Endress (1967) has shown that the Betulaceae are indeed very closely



related to the Hamamelidaceae, and that the two families have a large number of common characters, especially in the areas of floral structure and development. It is interesting to note that the Coryloideae (except *Corylus*) with the closest affinity to the Hamamelidaceae, have the same basic chromosome number,  $x = 8$ , whereas the other genera of the family with  $n = 14$  could possibly be derived from  $x = 7$ . On the other hand, on morphological grounds, the Betulaceae appear more closely related to the  $x = 12$  group of the Hamamelidaceae than to living members of the  $x = 8$  group, so that if Hamamelidaceae and Betulaceae are as closely related as suggested here, the lines leading to these families must have diverged before polyploidy became established in either one.

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P. G.

B. A. KRUKOFF CURATOR OF  
AFRICAN BOTANY  
MISSOURI BOTANICAL GARDEN  
2345 TOWER GROVE AVENUE  
ST. LOUIS, MISSOURI 63110

P. K. E.

BOTANISCHER GARTEN UND INSTITUT  
FÜR SYSTEMATISCHE BOTANIK DER  
UNIVERSITÄT ZÜRICH  
ZOLLIKERSTRASSE 107  
CH-8008 ZÜRICH, SWITZERLAND